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PINE NEEDLES, THEIR SIGNIFICANCE AND HISTORY

JEAN DUFRENOY

(WITH TWENTY-NINE FIGURES)

Are pine needles shoots or leaves? The question may still be debated, since neither the shoot nor the leaf has as yet been clearly defined. A review of the morphology, development, and physiology of the "needles" may be of interest.

Morphology

The definition given by VAN TIEGHEM (21), and usually adopted, is as follows: The leaf is symmetrical on both sides of a plane; the shoot is symmetrical around an axis. A needle is symmetrical on both sides of a plane, not around an axis; but by bringing into contact the different needles grouped at the end of a spur shoot, an organ is obtained which is symmetrical around an axis, and which therefore is a shoot. Needles, therefore, are fragmentary shoots. Anatomically they are polystelic shoots which have divided longitudinally into a variable number of parts¹ in order to increase the surface available for carbon assimilation. Being fragmentary shoots, the needle may be considered the homologue of the petiole of broad-leaved gymnosperms. The anatomy of the needle is strikingly similar to that of the petiole in *Ginkgo*, and we may quote COULTER (4) as follows: "The most ancient gymnosperms possessed ample fernlike leaves. . . . The conifers, however, have developed a very different type of leaf . . . which reaches an extreme expression in small and rigid needles."

The derivation of needles from fernlike phyllodes is apparent from anatomical data.

¹ That the different needles of a spur shoot are parts of the same organ is often strikingly evident. In most cases when a needle bends, the others bend also, so that all can be grouped into a cylindrical, though bent, shoot. When solitary, at the end of a spur shoot, needles are roughly cylindrical in form and shootlike, as normal needles of *P. monophylla*, and abnormal needles of *P. Pumilio* (STRASBURGER), *P. Laricio* (BOODLE 1), and *P. maritima* (DUFRENOY 13).

I. RELATION OF PINES TO CYCADS.—“Inverse wood,” such as occurs in the petioles of cycads, may be demonstrated on the ventral side of the protoxylem in juvenile leaves and needles of

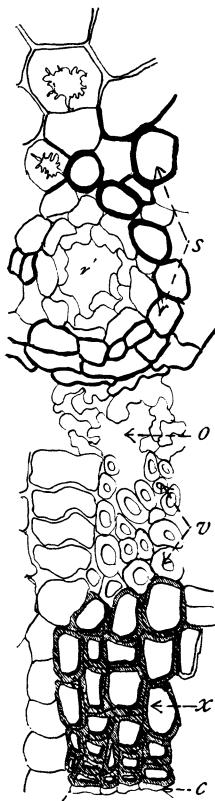


FIG. 1

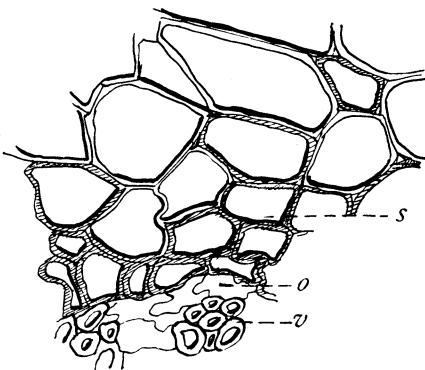


FIG. 2

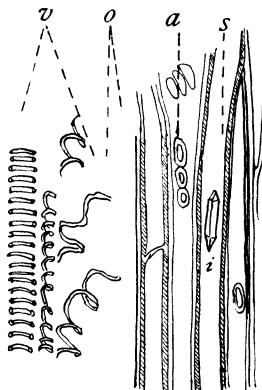


FIG. 3

FIGS. 1-3.—Transfusion sheath in needles of *Pinus maritima** (needle 2 years old, collected May 5, 1918, section 5 mm. above base): fig. 1, part of wood in vascular bundle; *c*, cambium, still dormant; *x*, wood of second year, vessels staining deep red with phloroglucin; *v*, wood of first year (protoxylem), spiral vessels, not staining with phloroglucin; *o*, lacuna; *s*, inverse wood, staining light red with phloroglucin, bright green with methyl green, orange with Sudan III; *r*, resin canal; fig. 2, detail of inverse wood (shaded tissue *s*), showing relation to protoxylem (*v*) and to pitted cells of periderm; *o*, lacuna; fig. 3, longitudinal section of same, showing spiral vessels of protoxylem (*v*) and inverse wood (*s*); *o*, lacuna; *a*, pitted vessels; *i*, oxalate of calcium.

* All the figures are from *Pinus maritima* collected at Arcachon.

P. maritima.² In normal needles, however, it is restricted to a few elongated vessels, sparsely distributed among pitted cells, from which they can be easily differentiated. They are always associated with peculiar elongated vessels which stain a bright orange with Sudan III (figs. 1-4). Tumors of *Coccus resinifans*, n. sp.,³ however, may result in the reversion of the vascular strand in the infected needles to the cycad structure, through the development

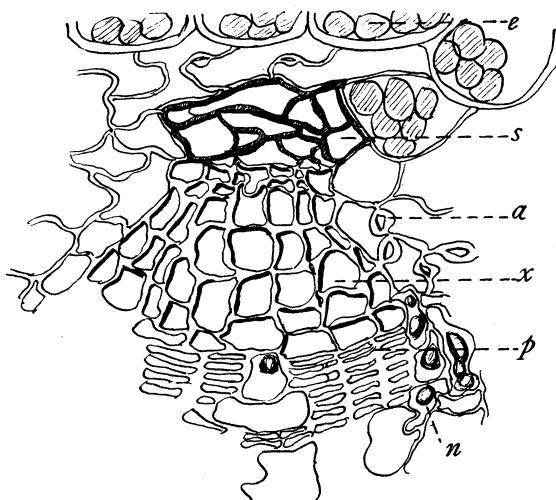


FIG. 4.—Part of periderm of young juvenile leaf (collected May 1918): *p*, phloem, with medullary rays (*n*) crowded with resin drops; *x*, normal wood; *s*, inverse wood in transfusion sheath, staining orange with Sudan III; *e*, endodermis.

of a well defined bundle of inverse wood, which may often extend from the ventral face of the protoxylem to the endodermis (figs. 5-16).⁴

2. RELATION OF PINES TO FERNS.—Other tumor-infected needles show phloem differentiating on the dorsal side of the inverted

² VAN TIEGHEM considered the transfusion sheath on the ventral side of normal wood in pine needles to be the homologue of the "inverse wood" in the petiole of cycads. Following TAKEDA (19), we found this untenable.

³ This *Coccus* has been recorded by DUFRENOY from stem tumors of pines, but the name was omitted from the note (13).

⁴ Stomatal anatomy also emphasizes the origin of cycads and pines from a common stock (REHFOUSS 18).

bundle of xylem, resulting in a fernlike state, comprising two bundles of xylem facing each other, with phloem outside (fig. 7). The relation of pines to the fern stock is further emphasized by the occurrence (in the wood or periderm of tumor needles) of all transitional forms, from normal pitted elements to scalariform cells, such as are present in ferns, and restricted to endodermal cells of normal needles.⁵

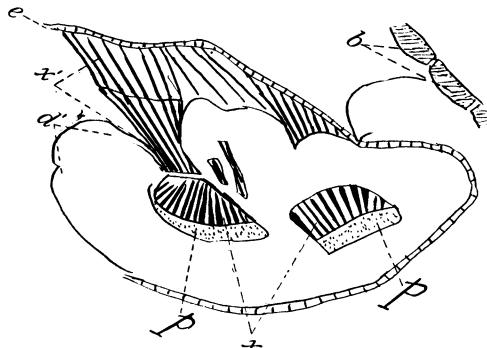


FIG. 5.—Tumor of *Coccus resinifans* on pine needle (collected at Arcachon, dunes of Abatilles, June 1917): part of periderm (schematic); *e*, endodermis, crowded with starch grains (starch and resin are much more abundant in tumor than in sound neighboring tissue); *d*, lignified cells of hyperplasia due to infection by *Coccus*; *b*, epidermis and hypodermis; *x*, normal wood; *p*, phloem; *x'*, inverse wood, composed of sclerenchymatous cells and fibers (staining red with eosin and green with methyl green) and of vessels staining orange with Sudan III; this inverse wood develops from ventral face of protoxylem to endodermis, and is homologous with inverse wood in cycads.

needles may be compared to the tracheae in Gnetales, and suggest the origin of both from a common fern stock.

4. RELATION OF PINES TO EQUISE-TALES.—The origin and evolution of the protoxylem is strikingly similar in pine

transitional forms, from normal pitted elements to scalariform cells, such as are present in ferns, and restricted to endodermal cells of normal needles.⁵

3. RELATION OF PINES TO GNETALES.—Scalariform cells in pine

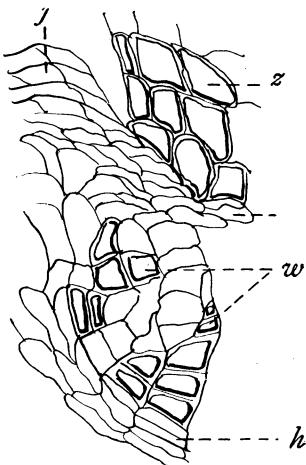


FIG. 6.—Part of fig. 5: *h*, phloem; *w*, lignified vessels in normal wood; *z*, same in inverse wood; *j*, lignified cells with hyperplasia.

⁵ The perforations in the scalariform cells of pines may be explained as derived from the fusion of enlarged bordered pits, as claimed by THOMSON for Gnetales; but the reverse is probably true, bordered pits being derived from ancestral simple incomplete perforations by acquiring highly specialized characters.

needles and in the stems of *Equisetum*, as it differentiates in both centripetally, from "pôles ligneux," and partially dissolves into lacunae.

The reappearance of polystelic organs, where the stele shows

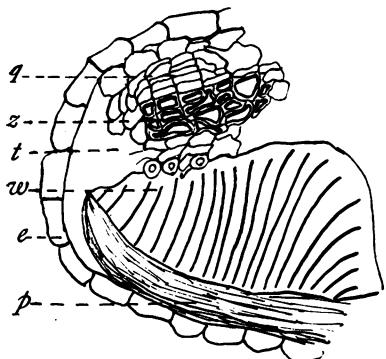


FIG. 7.—Half of vascular strand in tumor needle (collected November 1917): *e*, endodermis; *t*, periderm; *w*, normal wood; *p*, normal phloem; *z*, inverse wood; *q*, phloem.

Development

REJUVENESCENCE AND JUVENILE LEAVES.—Whenever a resting organ grows again, rejuvenescence must take place, and this is always observed in pines, either at the germination of the seed, or when lateral, dormant buds are caused to develop pathologically. When the pine seed germinates, cotyledons develop on the young shoot, and then single juvenile leaves.

These are smaller the higher up the shoot they develop, and at a certain height they are mere scale leaves. It is at the base of

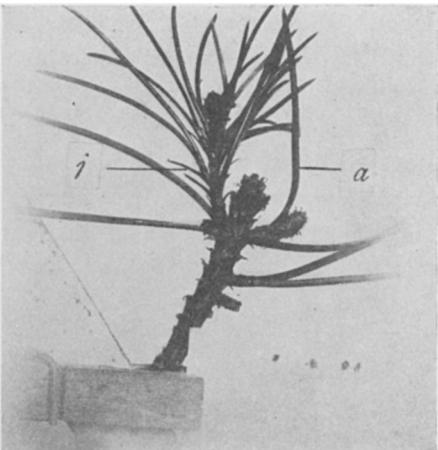


FIG. 8.—Proliferating spur shoots, springing up between the two geminate needles (*a*); *j*, juvenile leaf with spur shoot in axil.

these scales that the spur shoot of the needles arises. After it has developed a few scale leaves and a tuft of needles, this spur shoot generally remains dormant. If, however, the terminal bud of a branch happens to die, these lateral shoots may grow into a normal branch, bearing at first isolated juvenile green leaves and then scale leaves with spur shoots in their axils (fig. 8).

VARIATIONS IN THE NUMBER OF NEEDLES.—The number of needles on the spur shoot of each species is considered constant enough to be used as a character for classification; still, on rejuvenated or infected twigs, shoots are found which bear an unusual number of needles. BOODLE (1) makes the following statement: "In *Pinus monophylla* the spur shoots as a rule bear each a single needle, but two are occasionally present. MASTERS found by studying early stages that two leaf rudiments are always produced, but that one of them generally becomes arrested at an early stage."

Single needles have been observed by BOODLE on *P. Laricio*, and we found some on twigs of *P. maritima* that were infected by the larva of a xylophage insect (*Hylesinus piniperda*). These single needles are roughly cylindrical; in many cases a groove is present on one side of the leaf. On following it downward, it is found to contain two papillae, one of which is the apex of the spur shoot, the other the rudiment of the second needle. Variation in the number of needles in this case is due to arrest in the development of one of them. It is a rare occurrence in *P. maritima* and *P. Laricio*, but it has become the rule in *P. monophylla*. The multiplication of needles on the spur shoot has often been recorded on wounded, infected (13), or vigorous (20) shoots, and it has been regarded as a reversion toward ancestral, many-leaved gymnosperms (3).

Although these variations are somatic in origin, we have proved that they comply with Mendel's law, in that the proportion of bud mutations on the shoot is precisely that of F_2 recessives in the case of hybrids. Shoots of vigorous *P. maritima* or those infected with *Coccus resinifans* have been observed to yield 75 per cent normal 2-needed spur shoots, and 25 per cent 3-needed spur shoots. Proliferating spur shoots on *P. virginica* in Arcachon often yield 75 per cent normal 3-needed spur shoots, and 25 per cent abnormal

2-needed spur shoots, or vice versa (14). These bud mutations, like proliferating spur shoots,⁶ are due to modifications in the normal nutrition of the pine, caused by environmental factors, traumatisms, and chiefly parasites, and they result in increase of osmotic pressure in differentiating tissues.

That osmotic pressure is the ultimate determining factor is demonstrated by the fact that we were able to force 7-year old *P. maritima* to produce 3-needed spur shoots or proliferating spur shoots by watering abundantly, which of course increased tur-

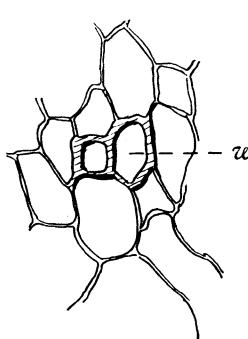


FIG. 9

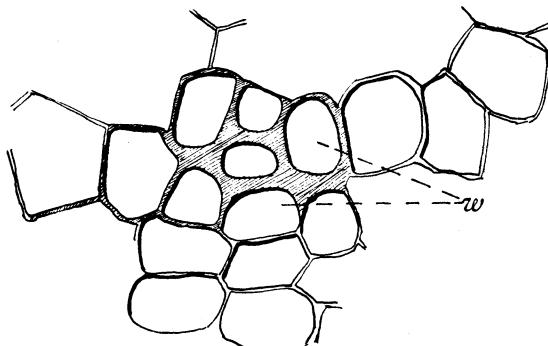


FIG. 10

Figs. 9-10.—Fig. 9, protoxylem in first needle appearing on juvenile pine: *w*, cells whose walls begin to show lignification and stain red with phloroglucin; fig. 10, protoxylem in very young needle of juvenile pine: section near apex; only one xylem pole.

gescence of cells. Whether needles or juvenile leaves develop depends upon the relative supply of soluble osmotic material to the cells. Needles, or all adult organs in general, develop from material obtained from the earth and atmosphere, by gradual assimilation. Juvenile leaves, or all juvenile organs in general, develop from material stored in the reserve tissue (9).

TRANSITION FROM JUVENILE LEAVES TO NEEDLES.—As needles and juvenile leaves are but different responses of the same organism to environmental factors, they may be assumed to show transitional

⁶ Development of lateral long shoots is exaggerated on pine seedlings exposed to sea wind, and results in "buissonnement," like that recorded by DEVAUX (6) for *Erica* on ocean dunes.

forms (contrary to the opinion of DAGUILLON 5). In fact, transitions are observed. The first needle to appear on juvenile pines shows anatomical features of juvenile leaves (figs. 9-17); and

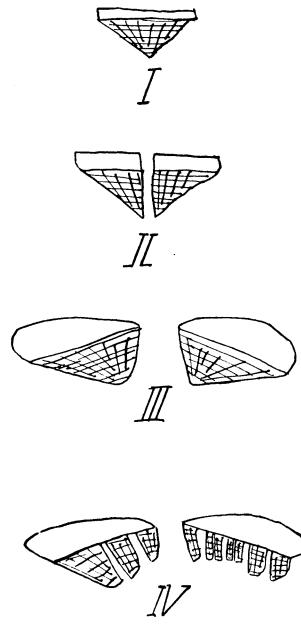


FIG. 11

FIG. 12

FIG. 13

FIGS. 11-13.—Fig. 11, transition from one vascular bundle to two semi-bundles in successive transverse sections from apex to base of needle: primary wood at apex (I) grouped into one bundle and like wood in juvenile leaves or in leaves of ancestral gymnosperms; with secondary structure, wood divides into two fragmentary bundles and becomes more like that in shoot (II-IV); fig. 12, stomatal cells of first needle produced on juvenile pine, showing structure of stomatal cells in juvenile leaves: no hypodermal cell present except below stomatal cells; letters as in fig. 13; fig. 13, stomatal and epidermal cells of needle on adult pine: *a*, cutin, staining orange with Sudan III; *l*, lignin, staining red with phloroglucin; *b*, thickening of epidermal cells, staining green with cotton blue; *c*, thickening of hypodermal cells; *h*, hypoderm; *e'*, epidermis; *s'*, stomatal cell (note local thinning of lignified wall, forming hinges).

transitions from one vascular bundle (as shown in juvenile leaves) to two semi-bundles (as typical of needles) is observed in successive sections of needles from the apex downward (fig. 11).⁷ Needles

⁷ The anatomy of needles varies so much from apex to base as to make all comparison worthless unless distance of the transverse section from the apex be clearly stated. The same statement applies to the age of the needle and the season when material is collected.

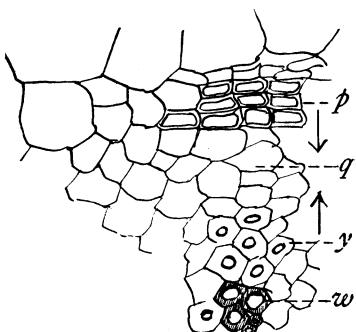


FIG. 14

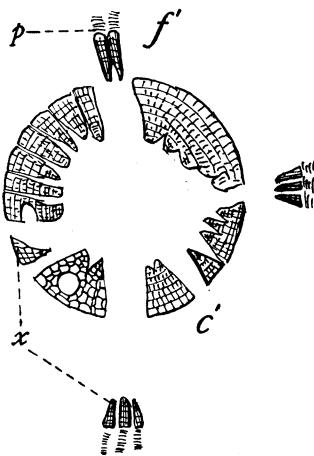


FIG. 15

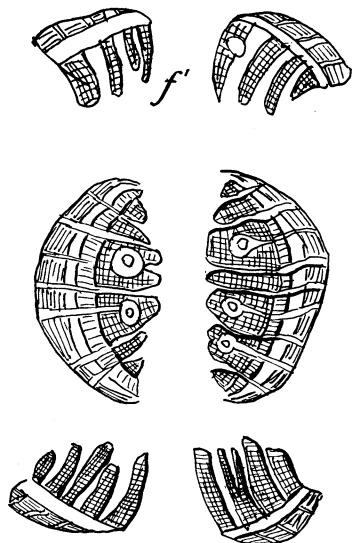


FIG. 16

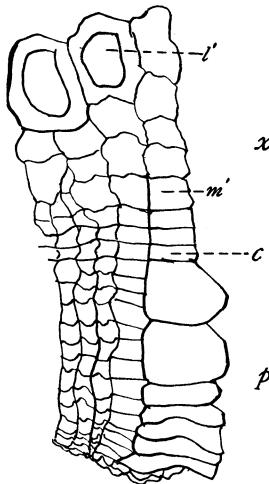


FIG. 17

FIGS. 14-17.—Fig. 14, periderm of very young juvenile leaf (collected April 25, 1918):

w, protoxylem; *p*, phloem; *y*, cells of future wood beginning to lignify; *q*, procambium; arrows indicate direction of differentiation; wood first differentiates centripetally and procambium becomes more narrow until finally it is a mere band of cambial cells; note identity of procambium in juvenile leaves and in first needles of juvenile pines (cf. *w*, figs. 9 and 10); fig. 15, course of vascular bundles in shoot of juvenile pine bearing juvenile leaves: *c'*, cauline vascular bundles; *f'*, foliar vascular bundles; *x*, xylem; *p*, phloem; fig. 16, course of vascular bundles in proliferating spur shoot: xylem inside (crossed lines), phloem outside, and cambium between, also resin canals and medullary rays; *f'*, foliar bundle consisting of 2 semi-bundles each divided by well defined medullary rays; fig. 17, part of foliar bundle (*f'*) in needle of proliferating spur shoot (collected May 3, 1918), part of *f'* of fig. 16: *c*, cambium active and producing spring wood above (*x*) and phloem (*p*) below; *l'*, wood vessels; *m'*, medullary rays; note that revegetation begins sooner in proliferating shoots than in normal spur shoots, which are still dormant at this season (cf. fig. 1).

may also be derived from juvenile leaves through such transitional forms as bilobed juvenile leaves (figs. 18-20) and concrescent needles⁸ (fig. 21).



FIG. 18.—Proliferating shoot bearing double (bilobed) juvenile leaves.

Histology

The chemical nature of the cell walls may afford good data for the comparison of pine needles with juvenile leaves or with phyllodes of other gymnosperms, living and fossil. Pine needles appear to be more differentiated histologically than morphologically,

18 tissues being recognized

from color reactions (see table I).

Physiology

Living cells must excrete poisonous materials which result from the disassimilation process (12). In the cells of pines these materials are resinous drops, which must be gotten rid of. In the primitive organs, resin probably filtered through the epidermis, and the epidermal cells were also secreting cells. This is still the

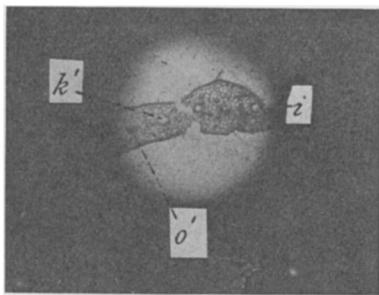


FIG. 19.—Transverse section of double juvenile leaf along plane ab of fig. 18; o' , double vascular bundles; k' , intraparenchymatous resin canals such as usually occur only in needles; i' , hypodermal resin canal typical of juvenile leaf; microphotograph, obj. 3.

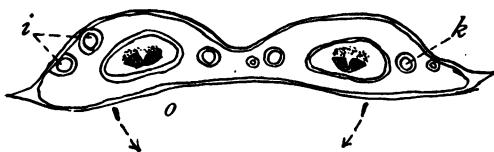


FIG. 20

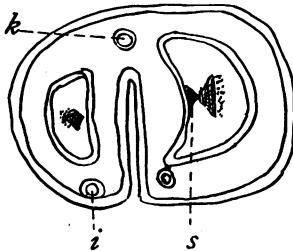


FIG. 21

FIGS. 20-21.—Fig. 20, schematic view of fig. 19: note that each vascular strand contains 2 semi-bundles, as in typical needles; fig. 21, concrescent or double needle: note hypodermal resin canals such as are typical of juvenile leaves, also inverse wood (s) on ventral side of protoxylem.

⁸ These concrescent needles have been considered the homologue of the double needles of *Sciadopitys*. They may be homologized with bilobed juvenile leaves bent as shown by arrows in fig. 20.

TABLE I

Histology of adult pine needle	Gentian violet	Methylene blue	Methyl green	Cotton blue*	Sudan III†	Phloroglucin	Devaux's method for pectose‡	Safranin in solution of ferrous chloride	HCl vapors
Cuticle.....	orange red
Epidermis: Middle lamella.....	red	deep blue	green	red	red
Thickening.....	light violet
Hypoderm: Middle lamella.....	red	deep blue	deep blue	red	blue	red	rose
Thickening.....	light violet	light blue	blue	red
Mesophyll.....	yellow red
Transverse walls of endodermis.....	deep green
Fibers around resin canals.....	blue
Periderm.....	light blue	rose
Transfusion sheath (inverse wood).....
Protoxylem (spiral vessels).....	red	bright orange	light red
Metaxylem.....	violet	blue
Phloem.....	red	deep red
Sclerenchymatous fibers.....	blue de Prusse
Cicatricial periderm in cankers.....
Resin drops.....	blue	light red
					orange or yellow

* Lactophenol solution. † Alcohol and glycine solution. ‡ Sections stained in ferrous chloride, then washed in distilled water, and treated with ferricyanide of potassium + HCl; pectose stain "blue de Prusse" (2).

case for the stamens and scales of pines, in which resin is excreted from the epidermal secreting cells. In juvenile leaves most epidermal cells become sclerenchymatous (to protect the parenchyma), and a very few still secrete resin (figs. 22, 23). Internal organs then differentiate, which can store resin, so that parenchymatous cells do not get poisoned, and resin canals run from the needles to the shoot and into the roots. The possibility of getting

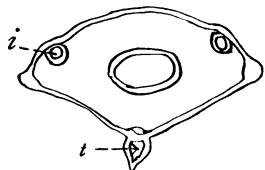


FIG. 22

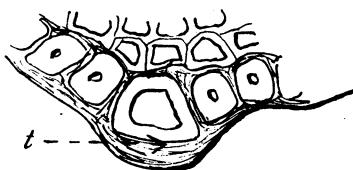


FIG. 23

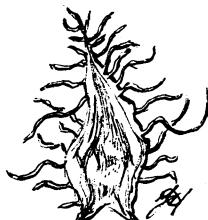


FIG. 24



FIG. 25

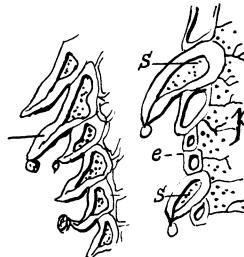


FIG. 26

FIGS. 22-26.—Fig. 22, abnormal juvenile leaf showing secretory hair (*t*) on ventral face; fig. 23, abnormal needles showing rudimentary secretory hair (*t*) on ventral face; fig. 24, scale leaf: strikingly similar to scale of *Cycas*; the hairs may be interpreted as sterilized ancestral ovules or stamens; fig. 25, juvenile leaf, showing hairs that may be interpreted as ancestral stamens, now sterile and secretory; fig. 26, secretory hairs of scale leaf (left) and juvenile leaf (right): *s*, secretory hair; *e*, epidermal cell.

rid of refuse poisonous material probably explains why coniferous trees are evergreen, whereas most of the other trees periodically lose their leaves and rest in winter.

Pathology

The needles of *Pinus maritima* may last 5 or 6 years. Often their death must be due to an accident, either a general trouble in the nutrition of the tree, or a local infection by rust or smut.

In the piñadas of Gascony, many of the needles which are infected in early spring by the aecidium of *Coloësporium senecionis* (*Peridermium oblongisporum* Kleb.) dry up and fall in summer. The "maladie du rouge" is very prevalent and the most important cause of the falling of needles, bringing ruin to many pine nurseries. It derives its name from the red patches that appear and spread on infected needles. It is due to several species of Asco-

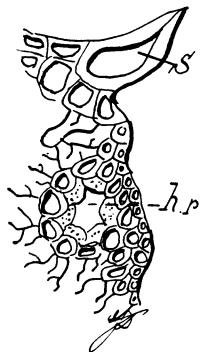


FIG. 27

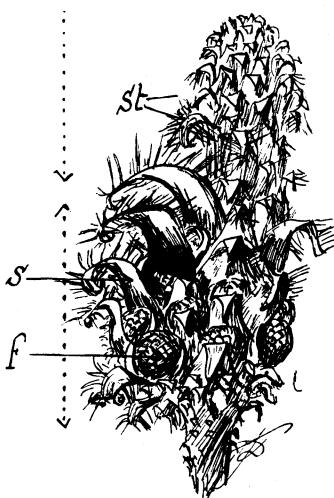


FIG. 28

Figs. 27-28.—Fig. 27, transverse section of juvenile leaf: *s*, secretory hair; *h.p.*, hypodermal resin canal; fig. 28, staminate cone of *P. maritima*: basal part, protected from sea wind by ridge in dune, normal and fertile (*s*, scale; *f*, flowers); upper part, exposed to sea wind, sterilized; collected on sand dunes of Arcachon, May 1917; note gradual reduction and sterilization of flowers from base upward.

mycetes: *Lophodermium pinastri*, which is the most common on several species of pine (*P. sylvestris*, *P. Pinea*, *P. maritima*); *Hypoderma pinastri*, the conidial form of which was observed by DUFRENOY on *P. maritima*; and *H. strobicola*, observed by FRON on *P. Strobus*.

Conclusion

Morphological variations are but the result of physiological variations (9). The different forms of the different phyllodes of pines, juvenile leaves, scale leaves, fertile leaves (δ and φ flowers),

and assimilatory organs (needles) differ widely; but abnormal transitory forms (figs. 24-28) which we have observed and described in previous works (9) allow us to state that all the forms of the different organs of pines are but different distorted features of a unique ancestral organ which, like the gametophyte of ferns, possessed at the same time the three different physiological functions of reproduction, assimilation, and protection (10, 11).

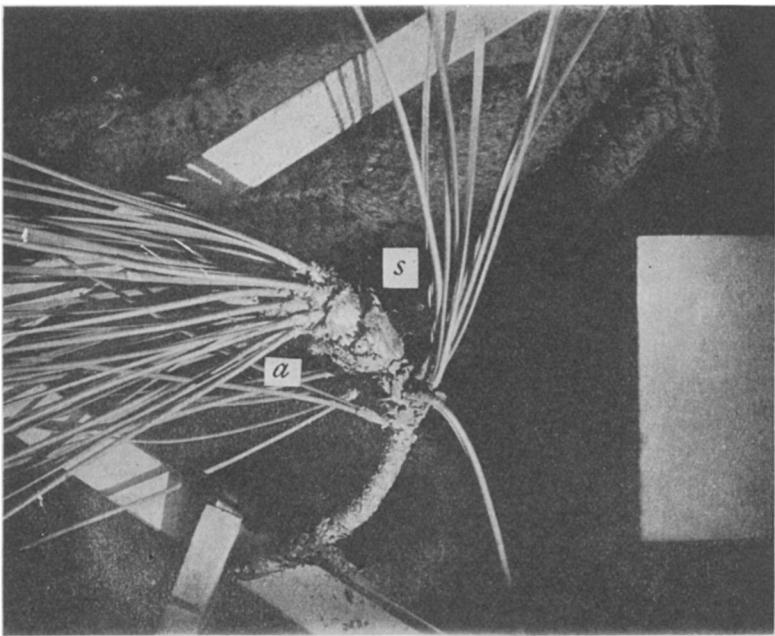


FIG. 29.—Photograph of ♂ inflorescence of *P. maritima*, shoot bent by sea wind; *s*, sterile scales on upper exposed side, with rudimentary ♀ flowers developing at base of scale in place of normal ♂ flowers; *a*, normal ♂ flowers on protected side; sterilization is gradual from protected to exposed flowers.

All the phyllodes of the primitive coniferous trees were probably fertile, and like the fertile leaf in *Cycas*, but under the pressure of unfavorable ecological conditions some parts became sterile scales. This is not mere formal hypothesis; such a sterilization has actually been observed. On the dunes of Gascony, for instance, the parts of the male flowers which are exposed to sea wind are sterilized (fig. 29), and scales develop in the place of stamens (8).

In like manner all the different organs must have descended from the ancestral organ; each lost the possibilities corresponding to the function it lost, but retained and perfected those which made it more adequately adapted to its special function. The following table shows how the different organs of pines may be derived from one another, according to data given by studies of abnormal, intermediate forms at the Biological Station of Arcachon.

Primitive organ	fertile (reproduction)	$\left\{ \begin{array}{l} \text{♂ fertile leaf} \\ \text{♀ fertile leaf} \end{array} \right.$
	green (assimilation) \rightarrow	juvenile leaf $\left\{ \begin{array}{l} \text{shoot} \\ \text{needle} \end{array} \right.$
		storage of reserves \rightarrow cotyledonary needle (7)
	self-protecting	\rightarrow scale

A needle which has specialized in the assimilation of carbon is itself a sort of assimilating organ; leaves of angiosperms are another.

Needles are the physiological leaves of pines. They differ from leaves in that they are perennial and are much less fragile. Typical leaves are temporary, delicate, perfectly shaped for intense assimilation, but unable to stand bad weather. Pine needles last several seasons. They have efficient xerophytic adaptation and can stand the roughest weather on arid lands, windy mountain tops, or storm beaten coasts (15, 16, 17).

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